Beyond pairwise mechanisms of species coexistence in complex communities

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Abstract: The tremendous diversity of species in ecological communities has motivated a century of research into the mechanisms that maintain biodiversity. However, much of this work examines the coexistence of just pairs of competitors. This approach ignores those mechanisms of coexistence that emerge only in diverse competitive networks. Despite the potential for these mechanisms to create conditions under which the loss of one competitor triggers the loss of others, we lack the knowledge needed to judge their importance for coexistence in nature. Progress requires borrowing insight from the study of multitrophic interaction networks, and coupling empirical data to models of competition.

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Beyond pairwise coexistence: biodiversity maintenance in complex communities

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Preface: The tremendous diversity of species in ecological communities has motivated a century of research on the maintenance of biodiversity, but much of this work examines the coexistence of just pairs of competitors. This pairwise approach ignores those coexistence mechanisms only emerging in diverse competitive networks. Despite the potential for such mechanisms to create conditions under which the loss of one competitor triggers the loss of others, we lack fundamental information needed to judge their importance for coexistence in nature. Progress requires borrowing insights from the study of multi-trophic interaction networks and coupling empirical data to mathematical models of competing species.

Introduction

The goal of ecological research on species coexistence is to explain how the tremendous diversity of species we see in nature persists despite differences between species in competitive ability[1,2]. However, empirically evaluating the interactions among a large set of competitors in nature is logistically challenging and many of the mathematical tools for analyzing the interaction between a pair of competitors do not readily translate to large networks of competing species[3]. As a consequence, coexistence research has focused overwhelmingly on mechanisms that operate between pairs of competitors. Although the focus on pairwise coexistence may prove valid, and great progress in understanding the maintenance of species diversity has been achieved with a pairwise approach[2] (Box 1), ecologists have had difficulty showing how the coexistence of many species in diverse ecosystems indeed results from pairwise mechanisms. How likely is it that over one thousand tropical forest tree species found in a 25 hectare plot in the Amazon coexist because of countless pairwise niche differences between the competitors[4,5]?

One tantalizing explanation for coexistence in species-rich communities involves mechanisms that only emerge in diverse systems of competitors. Indeed, systems of more than two competitors form a network of competitive relationships whose structure influences the dynamics of the system as a whole[3,6]. Whether studying species pairs in isolation can help us understand complex ecological networks is simply not known[7,8], reflecting broader challenges posed by complexity across the sciences. What is known is that network structure can strongly determine the robustness of mutualistic and multi-trophic networks to perturbations, and radically change the outcome of the pairwise interactions[9,10,11]. We might therefore expect similarly powerful consequences of embedding pairwise competitive interactions in diverse networks of competitors.

In this review, we argue that understanding the maintenance of species diversity requires ecologists to better explore coexistence mechanisms resulting from the structure of diverse competitive networks. We further argue that this understanding can be accelerated by applying lessons from the study of multi-trophic and mutualistic networks to competitive systems. Importantly, better understanding coexistence mechanisms that only emerge in diverse systems sheds light on the fundamental stability of biodiversity. By definition, these coexistence mechanisms erode as species are lost, meaning that the loss of one competitor may lead to the subsequent loss of still others, an extinction cascade well known from the theoretical study of trophic[12] and mutualistic[13,14] networks, but rarely studied in competitive systems (but see reference 15).

Here, we review the theoretical and empirical literature on mechanisms of coexistence that only emerge in networks of more than two competitors. Although these mechanisms were demonstrated nearly a half century ago, convincing empirical tests of their operation remain rare, leaving the implications of these interactions for coexistence in nature unknown. Though we focus exclusively on the interactions between competitors, throughout the review, we highlight findings from the study of trophic and mutualistic networks that shed light on how diverse competitive networks operate and can be analyzed. Last, we lay out a roadmap for advancing understanding of coexistence mechanisms that only emerge in systems of more than two species. This involves developing a predictive understanding of when these mechanisms are likely to operate, empirically evaluating their prevalence and importance in nature, and theoretically demonstrating how they influence coexistence in truly diverse systems.

Coexistence between more than two competitors

Theory shows two kinds of competitive dynamics that only emerge in networks of three or more species: "interaction chains" and "higher-order interactions" (Fig. 1). These interactions are not necessarily stabilizing, and can in fact destabilize coexistence. Therefore, we first define these interactions and then explain the conditions under which they promote species richness, our measure of diversity for this review.

Interaction chains emerge when pairwise competitive interactions are embedded in a network of other (still pairwise) interactions. As in a trophic cascade, the resulting indirect effects arise from changes in the density of a third species (or more) which interacts with both species of the focal

pair (Fig. 1b). Even when all direct pairwise interactions are negative, these indirect effects are often positive, mediated via reductions in the density of shared competitors[16] (Fig. 1b). As explained in the next section, the best-studied stabilizing competitive network involves intransitive competition among three species, as in a game of rock-paper-scissors[6,17]. While the interactions between the species remain fundamentally pairwise, the stabilized dynamics emerge from stringing these pairwise interactions together, so that changes in density propagate through the network forming a negative feedback loop that counteracts the initial perturbation.

Higher-order interactions emerge when the interactions between species are no longer fundamentally pairwise. Instead, the per capita effect of one competitor on another depends on the population density of a third, fourth, or fifth species, etc. (Fig. 1c). These interactions are analogous to trait-mediated indirect interactions in the trophic literature, where higher-order interactions occur when a predator for example, modifies the behavior of its prey with cascading effects on even lower trophic levels[18]. Higher-order interactions among competitors are less intuitive than interaction chains, but can emerge when one species has a plastic morphological or behavioral response to another (e.g. the reduction in forb rooting depth in Fig. 1c), which alters its competition with a third species. For example, plantain suppresses the root growth of red fescue, an otherwise efficient competitor for soil nutrients[19]. This plastic response would, in turn, weaken the per capita effect of red fescue on the performance of other nutrient limited competitors. More generally, higher-order interactions might be hypothesized to stabilize coexistence when the presence of one species weakens the interspecific interaction between another two.

The distinction between interaction chains and higher order interactions is determined by whether the indirect effect emerges from a change in competitor density (interaction chain) versus a change in per capita competitive effects (higher-order interaction). As a consequence, interaction chains and higher-order interactions differ in the timescale of their operation. With a higher-order interaction, one competitor immediately modifies competition between another two (by changing individual traits for example). By contrast, with interaction chains, it does so via adjustments to the density of the other competitors and should therefore emerge with a greater time lag. Though distinct in principle, interaction chains and higher-order interactions both require diversity to operate, and thus both can underlie extinction cascades that determine the robustness of biodiversity to environmental perturbations. The simplest example of this dynamic involves the loss of one competitor from a system stabilized by intransitive competitive loops, which leads to the loss of others (Fig. 2).

Interaction chains- theory

Theoretical ecologists have long been aware that the outcome of pairwise competitive interactions can change when species are embedded in a diverse competitive network. Much of this understanding was initially inspired by studies of Lotka-Volterra systems describing the interactions between a diverse set of species- often modeling the response of entire communities to small perturbations around an equilibrium[15,20,21] (Lyapunov local asymptotic stability, Box 2). Subsequent work showed that when interspecific competitive interactions are randomly sampled from a distribution, more diverse communities are less likely to be stable[22]. Although this result suggests that coexistence opportunities are reduced by increasing the number of species, it is

159 partly a function of the resulting random network structure- other intransitive competitive
160 structures can alter this expectation, as explained below.
161
162 A parallel course of study has explored the specific competitive relationships, or network
163 structure in today's language, that allow the outcome of competition between two species to be
164 altered by the inclusion of a third competitor (or more)[16,23,24,25]. The inclusion of this third
165 competitor can benefit coexistence by playing a fitness equalizing or stabilizing role (as defined
166 in Box 1). For an example of the former, a superior competitor can favor the coexistence of two
167 others by differentially harming the fitter of the two[24]. With this interaction structure, the
168 superior equalizes the average fitness of the other two competitors, but does not stabilize their
169 dynamics through the introduction of a novel coexistence mechanism. Any long-term
170 coexistence would still require pairwise niche differences as defined in Box 1. By contrast, when
171 the three species form an intransitive competitive loop, this structure can stabilize
172 coexistence[23,25].
173
174 Intransitive competition, as in the game of rock-paper-scissors, occurs whenever species cannot
175 be ranked in a simple linear competitive hierarchy. This mechanism is stabilizing because
176 decreasing the abundance of any one competitor in the loop propagates through the network in a
177 way that feeds back to favor its recovery. These stabilized dynamics, however, only emerge in
178 systems with an odd number of species[6]; this mechanism cannot produce coexistence among an
179 even number of competitors, raising interesting questions about how these systems assemble.
180 The simplest models of this type of interaction are those in which competitive dominance
181 between species is encoded in a directed graph, where nodes represent species and for each pair,

an arrow, termed an "edge" connects the competitive winner to the loser[26] (Fig. 2a). The simplest case of intransitive competition, in which three species form a rock-paper-scissors intransitive loop has been shown to generate possible coexistence of the three competitors, albeit with cycles[26]. Larger networks containing many species have been explored by simulation[27] or by writing deterministic equations[6], such as the replicator equation central to evolutionary game theory[26] (Fig. 2b).

With other modeling approaches to interaction chains, competition is less asymmetric, yet intransitivity among three competitors still strongly stabilizes dynamics. For example, May and Leonard[23] studied a Lotka-Volterra model for three species where competition coefficients were chosen such that species A is more affected by B than vice versa, B is more affected by C than vice versa, and C is more affected by A than vice versa. Thus, all coefficients are negative, but those with the largest magnitude are arranged as in a rock-paper-scissors loop. Such a model can produce robust limit cycles of all three species rather than the monodominance expected under transitive competition. Similar mechanisms promote coexistence in models with explicit consumer-resource interactions[28] successional replacement[29], or a competition-colonization-space preemption tradeoff[30].

Although the specific effects of intransitive competition illustrate the significance of embedding pairwise competitive interactions into a diverse network of competitors, how network structure in the more general sense affects the dynamics of diverse competitive communities is rarely explored explicitly. Nonetheless, an implicit acknowledgment of the importance of network structure comes from the common practice of theoretical ecologists to build communities of

205 competitors from rules that generate specific interaction structures[31]. Models often assume, for
206 example, that the per capita effect of one species on another is a function of their overlap in
207 resource use along a common niche axis[31]. Moreover, network architecture is well known to
208 strongly influence species persistence in other types of interaction networks. Food webs, for
209 example, tend to be organized in compartments, where species within a compartment interact
210 more frequently among themselves than they do with species from other
211 compartments[32,33,34,35,36, but see 37]. Interestingly, this block structure can buffer the spread of
212 perturbations across the entire network[12,22], and could play a similar role in networks stabilized
213 by intransitive competitive relationships. Networks of mutualistic interactions such as those
214 between flowering plants and their animal pollinators or seed dispersers, tend to be organized in
215 a nested manner which means that specialist animals interact with proper subsets of the plant
216 species interacting with more generalist animals[38]. This nested network structure can increase the
217 number of coexisting species in mutualistic networks[39].
218
219 In one of the only contemporary studies to explicitly ask how network structure affects
220 competitor dynamics, Barabas et al.[3] explored how the arrangement of coefficients in the
221 interaction matrix (Box 2) affects the stability and feasibility of diverse competitive systems.
222 They found that both maximal and minimal stability were achieved by arranging the interaction
223 coefficients in a nested manner, and arranging them in blocks. This work shows that macroscopic
224 network properties such as compartmentalization and nestedness likely play central roles in
225 competitive communities as known for other interaction types.
226
227 *Empirical evidence for intransitive competition*

Interaction chains among competitors can have a range of effects on dynamics within competitive networks[24], though of particular relevance here are interaction chains that specifically act to stabilize coexistence – intransitive competitive loops. Direct empirical evidence that intransitive competition operates in nature is generally sparse, and studies reporting strong evidence for transitivity, and studies reporting pervasive intransitivity both have underlying problems. The two most convincing examples of intransitive interactions actually concern competition within, not between species. Kerr et al.[17] showed intransitive interactions among engineered strains of *E. coli*, while Sinervo and Lively[40] demonstrated these interactions among individuals with different mating strategies within a lizard population. Bridging the within to between species evidence for intransitivity are Lankau and Strauss[41], who showed intransitive competition between two selectively bred populations of a mustard species and a third, heterospecific plant competitor. However, their mathematical models suggest that in nature, selection should drive the mustard population to a single optimal strategy, collapsing the system to pairwise between-species coexistence[42]. The best species-level evidence for intransitive competition comes from patterns of colony overgrowth in marine sessile organisms[43,44,45]. Even in these systems, however, the observed intransitive competition among a triplet of species is embedded in a larger matrix of mostly transitive interactions.

An alternative approach to evaluating the prevalence of intransitivity involves analyzing the results of experiments where many species, typically plants in greenhouse settings, compete against one another in pairwise trials. Although these studies have generally concluded that intransitivity is rare[46, 47,48,49,50,51], they generally measure competitive dominance with relative yield or related measures, where the growth of an individual with a heterospecific neighbor(s) is

scaled by its growth with neighbors of its own species. This approach measures differences between species in their per capita competitive effect on the common target individual (Supplementary Notes). However, both mechanistic and phenomenological models show that competitive dominance arises not from species differences in their per capita competitive effect, but instead by their ability to tolerate the effects of intra and interspecific competitors[2,52]. Relative yield provides no insight on how species tolerate competition, and therefore cannot reveal competitive outcomes (Supplementary Notes).

An alternative approach developed by Ulrich et al.[53] back-infers the network of pairwise competitive dominance from patterns of species abundance in field plots. Applications of this approach have suggested widespread intransitivity in plant communities and a positive relationship between the degree of intransitivity and species richness[54]. However, the method is built on assumptions of low spatial environmental heterogeneity and density-independent probabilities of species replacement, and thus the inferred competition matrix does not allow for pairwise niche differences (Box 1). While the approach may be appropriate for asking which intransitive network structure is most consistent with patterns of abundance assuming no other controls on species abundance, it is not well suited for evaluating whether intransitivity is a more parsimonious explanation for abundance patterns than pairwise mechanisms.

In sum, the existing empirical literature on intransitive competition consists of several well resolved within-species but not between-species examples of intransitive loops, analyses of competition experiments based on improper estimates of competitive dominance, and inverse modeling premised on the absence of pairwise niche differences. Evidence offered by these

approaches makes it difficult to resolve the prevalence of intransitive competition in nature. However, prevalence is only half of the problem, the other half being the degree to which observed intransitivity stabilizes coexistence in nature, for which the absence of evidence is more glaring.

Higher-order interactions- theory

The assumption that the interaction between species is fundamentally pairwise is central to nearly all coexistence theory. As explained in the subsequent section, from an empirical standpoint, we simply have little idea whether this assumption is correct. Species interactions may actually be three-way, four-way, etc. Abrams[55] has shown that higher-order interactions commonly emerge in classic models of resource competition with non-logistic resource growth or nonlinear functional responses of the consumer to resource density. This result raises the important point that the designation of higher-order interactions as something fundamentally different than pairwise competition is partly an artifact of our typically phenomenological approach for studying species coexistence. This approach uses interaction coefficients to describe the negative effects of one competitor on the other, rather than explicit interactions with shared resources or consumers as in more mechanistic models of competition (e.g. reference 52). In these mechanistic models, higher-order interactions can emerge organically from the underlying biology without the addition of special higher-order terms[55]. However, regardless of whether one considers phenomenological or mechanistic models of competition, the question of how much the interaction between any two species is dictated by other species in the system remains relevant.

296 Recent theory has shown how a network framework can be used to study higher-order
297 interactions[56]. Rather than a graph in which arrows connect species (nodes), as in networks of
298 pairwise interactions, higher-order interactions are represented in a hypergraph, where arrows
299 connect species (nodes) to other arrows (as in Fig. 1c). Just as an $n \times n$ matrix of pairwise
300 interactions is used to parameterize a system of equations for two competitors, one can use a $n \times$
301 $n \times n$ tensor (multidimensional array) to describe three-way interactions, where each element
302 describes the joint effect of two species on the third[57]. Though such a tensor describes all higher
303 order interactions that can operate in principle, their actual operation in nature is complicated by
304 the finite nature of individuals and the fact that sessile organisms only interact with those in their
305 neighborhood[4]. At the same time, stabilizing effects of higher order interactions (and interaction
306 chains) could potentially compensate for the depressive effects of demographic stochasticity on
307 species richness.
308
309 Despite common arguments that higher-order interactions should be pervasive in ecosystems[58,
310 59], they are generally excluded in models of competition. Ecologists therefore lack clear
311 expectations for how such interactions should affect the outcome of competition. Moreover,
312 given the dearth of empirical evidence for how these interactions are structured, theory has few
313 anchor points from which to work. Therefore, a reasonable starting point is to consider the
314 implications of random higher-order interactions, as in the recent work of Bairey et al.[57]. These
315 authors show that the inclusion of interactions of increasingly higher-order, with randomly
316 assigned values, reverses May's[20] classic result that community diversity destabilizes ecological
317 systems. With strictly four-way interactions, more diverse communities can better withstand the
318 destabilizing effects of stronger interactions, and as a consequence, the loss of a species makes

the remaining system more vulnerable to extinctions. Bairey et al.[57] explore the stability of communities that are a mix of competitors, consumers, and mutualists, though similar results might be expected to hold for purely competitive systems. Still, this work should not be interpreted to suggest that higher-order interactions are necessarily stabilizing. As with interactions chains, the consequences of higher order interactions should depend on the structure of the network and the nature of the higher-order effects, topics yet to receive considerable empirical attention (but see reference 59).

Higher-order interactions- empirical evidence

Although higher-order interactions between species in different trophic levels are the subject of considerable research[56], such interactions among competitors, our exclusive focus here, are far less understood. The classic approach for evaluating the operation of higher-order interactions between three species- the scope of existing work- involves evaluating the performance of species in all two and three way combinations[60,61,62,63]. The number of treatments typically restricts these experiments to tractable laboratory systems- fruit flies, protists, and pond microcrustaceans, for example. With this design, one then tests how well the response of a focal species to each of the others in isolation (pairwise competition) predicts the focal species' response to multiple competitors (in the triplet), typically tested with an analysis of variance. However, several authors have shown that ANOVA tests can generate a significant statistical interaction between the effect of two competitors on a focal species, and therefore the suggestion of higher-order interactions, even when the effect of each species on the focal is independent of the other[7,64,65]. Moreover, in experiments conducted over a time frame long enough for competitor densities to change, it is difficult to prove that the apparent higher-order interaction is

342 not actually caused by a change in the abundance of the competitors, and is actually a
343 "misdiagnosed" interaction chain[62,64]. As a consequence of this, as well as their laboratory
344 settings, these experiments have not provided definitive tests of whether higher-order
345 interactions are prevalent in ecological communities in nature (but see reference 63).
346
347 A related approach involves fitting population dynamic or biomass accumulation models to
348 competition experiments and evaluating how well a model with purely pairwise interactions can
349 predict the performance of individuals or dynamics of multispecies systems[59,66,67]. Quantifying
350 higher-order interactions with this approach is a formidable empirical and statistical challenge: if
351 characterizing pairwise interactions requires empirically estimating n^2 coefficients (n being the
352 number of species), estimating all triplets requires up to n^3 coefficients. To simplify the design,
353 Weigelt et al.[67] grew a single focal plant species in experimental arrays surrounded by
354 conspecific individuals, or individuals belonging to a single, two, or three other species. They
355 then fit a series of models to describe how focal species biomass was reduced by neighbors.
356 They showed that in one third of the three or more competitor combinations tested, a model with
357 an interaction term in addition to pairwise effects best described individual biomass decline with
358 neighbor density, suggesting higher-order interactions. More direct statistical tests for higher
359 order interactions were developed by Mayfield and Stouffer[59], who then applied their method to
360 observational data collected in a community of annual plants in southwestern Australia. They
361 found that higher order interactions significantly affected the fecundity of three of six focal
362 species, often weakening the suppressive effect of neighbors.
363

Aside from the technical challenges of quantifying higher-order interactions, a central problem in this literature is that few empirical studies actually evaluate the ecological significance of these interactions. Indeed, prior authors have argued that because higher-order interactions almost certainly operate in nature (demonstrating them is just a matter of having enough degrees of freedom), the real question is whether higher-order interactions have consequences noticeable against a background of other sources of ecological uncertainty[68]. Unfortunately, how higher-order interactions influence coexistence is difficult to assess because few studies measure response variables that can be translated into dynamics through a competitive population dynamics model. In sum, ecologists may have modestly better evidence to evaluate higher-order interactions than intransitive competition, but evidence is still sparse and how these interactions modulate community dynamics in nature is very difficult to evaluate with current work.

Moving forward with n-species

Advancing our understanding of coexistence mechanisms that only operate in systems with more than two competitors requires three types of knowledge gain. First, we need better expectations for when and how intransitive competitive relationships and stabilizing higher-order interactions emerge in competitive communities. Second, we need definitive empirical evidence concerning the prevalence and importance of these interactions in nature. Finally, we need theoretical guidance for how these mechanisms influence coexistence in truly diverse communities. In what follows, we lay out a research agenda to resolve these major outstanding questions.

When to expect complex coexistence mechanisms

Much of the work on interaction chains and higher-order interactions has emphasized phenomenological models of competition. For theoreticians, these models allow one to efficiently evaluate the consequences of these interactions for coexistence, and for empiricists, the models present a limited number of parameters for fitting to data. However, inserting higher-order terms or intransitive competitive loops into phenomenological models does not develop a predictive understanding of when intransitive competition and higher-order interactions emerge in nature. Developing this understanding is important because quantifying these mechanisms is challenging and we only want to do so when we have reason to believe they operate strongly. Moreover, higher-order interactions need to be demystified if they are to become a regular part of how ecologists conceive of coexistence, and identifying their mechanistic basis is one way of doing so. To illustrate the extent of the problem, even empirical studies arguing for the operation of higher-order interactions have only rarely provided a mechanism for the observed interaction (for exceptions, see reference 63 and 67). We therefore advocate exploring mechanistic models of competitive interactions in diverse networks that explicitly incorporate the dynamics of resources and/or predators.

The value of this more mechanistic approach for understanding intransitive competitive relationships has already been demonstrated by the work of Huisman and Weissing[69]. They built consumer resource models and demonstrated the conditions under which transitive and intransitive competition emerge in systems of three species. They showed that multiple limiting resources, an important condition for coexistence via pairwise niche differences, are also required for the emergence of intransitive loops. With only a single limiting resource, species are simply ranked by their ability to depress that resource, generating purely transitive competitive

410 relationships (a point reinforced by reference 6). Similar approaches could be applied towards
411 understanding the conditions necessary for the emergence of higher-order interactions, and
412 whether these interactions benefit or harm coexistence. Initial progress towards this goal could
413 be achieved by using existing models of resource competition such as Tilman's[52] R* model to
414 explore (1) when higher-order interactions emerge in a system with more than two competitors,
415 and (2) if they do emerge, how they affect coexistence and extinction cascades. Assumptions
416 about trait plasticity in such models may prove important; thus existing eco-evolutionary models
417 where trait values respond to and affect competitive interactions[70] may be a useful starting point.
418
419 Of course, adding resources or higher trophic levels to models with a diverse guild of
420 competitors adds network complexity and quantitative challenges. Fortunately, techniques exist
421 to simplify the structure of multi-trophic systems by "correcting" the competition coefficients so
422 that they include both within and between trophic level interactions. Bastolla et al.[71] developed
423 such a framework, allowing one to calculate an upper limit to the number of coexisting species in
424 competitive systems. This framework was later extended to address systems of species that
425 compete and engage in mutualistic interactions. They found that the structure of the mutualistic
426 interactions affects species coexistence by modulating the relative effects of facilitation and
427 competition[39]. Methods also exist for reframing the effects of network structure in terms of
428 average fitness differences and stabilizing niche differences (as defined in Box 1), metrics
429 commonly used to understand pairwise coexistence. For example, Jabot and Bascompte[72] have
430 shown how the balance between the stabilizing effects of interactions with higher trophic levels
431 and effects of interactions that drive fitness differences are mediated through the structure of the
432 multi-trophic interaction network.

Obtaining the needed empirical evidence

The general absence of evidence to evaluate the prevalence and importance of interaction chains and higher-order interactions in nature may be one of the greatest knowledge gaps in our study of species coexistence. Filling this gap requires two equally important efforts: (1) quantifying the operation of these mechanisms in natural communities, and (2) evaluating their importance for species coexistence. We believe that moving forward on both these fronts requires fitting multispecies population models to observational or experimental data. We acknowledge that a model-based approach may not be necessary for laboratory populations of micro-organisms, where one has the option of comparing the "long term" competitive outcome of species in pairwise and more complex competition trials[8]. Nonetheless, without fitted models, it remains difficult to resolve exactly why outcomes change as community complexity increases.

The model-based approach can be implemented in multiple ways, but at its core, employs two steps (Fig. 3). The first step involves using statistical models to quantify how the demographic performance of individuals depends on naturally occurring or experimentally imposed variation in the abundance and identity of neighbors[73,74,75]. The fitted models can then be used to quantify the prevalence of intransitive competition[76] or the significance of higher-order terms[59]. The second step involves using models to project community dynamics based on the fitted relationships[75,77] (Fig. 3). These projections can be based on analytical expressions, or multispecies simulations of stage or age structured demographic models. One can then quantify the importance of a particular mechanism for coexistence by projecting the outcome of competition in the presence and absence of that mechanism. An alternative option is to construct dynamical models that differ in the mechanisms they include and directly fit these to observed

456 abundance changes. However, some coexistence mechanisms with only weak statistical support
457 may nonetheless strongly influence dynamics[77], necessitating the model fitting followed by
458 projection approach advocated here.
459
460 For an example of how one might project fitted models to quantify the consequences of higher-
461 order interactions- something no empirical study has yet accomplished- one can compare
462 community dynamics projected under the assumption of purely pairwise interactions to dynamics
463 when fitted higher-order interactions also operate. Similarly, to understand how well intransitive
464 competition stabilizes coexistence, one can force the pairwise intraspecific interactions to match
465 the interspecific interactions (as in references 75 and 76), leaving only the intransitivity to
466 stabilize dynamics.
467
468 Despite the need for mathematical models fit to empirical data, building them presents
469 formidable challenges. Perhaps the most obvious challenge is parameter estimation and the risk
470 of overfitting the models[59]. In addition to parameters describing intrinsic demographic
471 performance, which may vary with size, stage or age and in space and time, we require
472 parameters describing intra- and interspecific density dependence. As noted earlier, the number
473 of these pairwise interactions increases as the square of the number of species in the system, and
474 the number of higher-order interactions expands even more rapidly. To properly estimate these
475 parameters, ideally we would observe the per capita growth rate of each species in the
476 community for all density combinations of the constituent species, essentially an n-dimensional
477 response surface design. Observational datasets will often fall short of this ideal (with high risk
478 of overfitting), especially if stabilizing mechanisms maintain populations close to some

equilibrium. Therefore, experiments that manipulate the densities of multiple competitors in a factorial design and examine their pairwise and interactive impact on individuals of a target species likely present the most convincing option for fitting higher-order interactions in nature.

Coexistence in diverse competitive networks

How intransitive competition and higher-order interactions influence coexistence and the robustness of competitive networks to species loss in systems larger than those we can empirically parameterize deserves further theoretical attention. With this goal in mind, progress is hindered by the fact that while we can evaluate the stability of systems with *n* competitors, the classic focus of theory (Box 2), we cannot easily evaluate how many of those competitors can coexist if the full system is unstable. We therefore advocate a shift in focus from the probability that *n* species coexist to how many species will coexist if we start with *n*. One could then ask, for example, how higher-order or intransitive interactions dictate the fraction of species that can coexist after community disruption and recolonization, a common scenario in some ecological systems[78,79].

Simulation cannot easily be used to achieve these aims due to the tremendous number of sub-communities that can be derived from a truly diverse system. Therefore, quantifying the fraction of species that can coexist requires building new theory, designing different experimental protocols, and drawing on mathematical tools new to ecology. Currently, this coexisting fraction is only known for highly-idealized models of competition where all pairwise interactions result in exclusion so coexistence is only possible through intransitive competition. If one determines the pairwise winner and loser at random, building what is called a "random tournament graph",

the number of coexisting species when starting with n can be calculated analytically[6]. While the probability of having all species coexist becomes vanishingly small with increasing n, on average $n / 2$ species coexist. Hence, one can have a very diverse system despite having lost a number of species to extinction.

Finally, a theoretical framework that predicts the fraction of species that can coexist would be particularly useful for evaluating how network structure influences the extent of extinction cascades. More formally, if n species stably coexist, but $n - 1$ do not (due to the loss of a key competitor), ideally we could predict the fraction of the $n - 1$ species that persist. Moreover, how this fraction depends on the structure of the competitive network including the structure of both interaction chains and higher order interactions provides important questions for future research. Analyses already developed for the study of mutualistic and multi-trophic networks[9,10,39,80] could prove particularly valuable here.

Before we get too carried away…

We have argued that ecologists lack the empirical data to evaluate the stabilizing role of intransitive competition and higher-order interactions in shaping species coexistence. While theory shows potentially critical roles for these types of interactions in shaping species coexistence[6,57], our call for appropriate empirical tests should not be taken as an expectation that these factors play important roles in nature. We simply do not know. Moreover, other types of evidence can be used to bracket their potential importance. As noted at several points in this review, one unifying feature of coexistence mechanisms depending on intransitivity or higher-order interactions is that they depend on the presence of a sufficient number of species to

operate. However, a large body of studies experimentally manipulating species diversity suggests that the more species one assembles in a community, the more difficult it is for new species to enter[81]. This result may reflect the fact that traditional pairwise niche mechanisms, which would generate this pattern, overwhelm the operation of coexistence mechanisms that only emerge in large communities.

A second reason for caution is that ecologists do have reasonable alternatives relying purely on pairwise mechanisms to explain the very high diversity seen in many ecosystems. Spatial environmental heterogeneity is a powerful force maintaining species diversity, even at surprisingly small scales[82]. Although it may seem improbable that each species in diverse communities has specific environmental preferences, modest differences between species can maintain coexistence so long as their average fitness is similar (Box 1). Of course, coexistence in nature may also result from the interaction between pairwise mechanisms and those that require more than two species. Spatial heterogeneity in intransitive competitive relationships[6] or heterogeneous mutualistic and antagonistic network structure[72] can strongly benefit regional scale coexistence. In addition, the cyclical nature of coexistence under intransitive competitive loops creates temporal environmental variation on which many other species can specialize and ultimately coexist[28].

Conclusions

In this review, we have argued that coexistence mechanisms that only emerge in systems with more than two competitors present a largely unexplored control over the maintenance of diversity in species rich communities. We have pointed out that when studying more than two

548 competitors, ecologists necessarily confront an ecological network, yet how the structure of that
549 network influences coexistence is unknown. The sparseness of evidence results from the
550 intractability of empirically evaluating competition among many species and the technical
551 difficulties inherent in tightly coupling theory to data. Despite these challenges, there are
552 compelling reasons to deepen our understanding of these more complex coexistence
553 mechanisms. Armed with recent advances in data-driven modeling and network analyses
554 developed for multi-trophic systems, ecologists are well-positioned to answer, for some species
555 rich communities at the very least, how much of their coexistence results from mechanisms that
556 only emerge in diverse systems. Few other questions in ecology have such great potential to
557 radically shift how we think about the maintenance and fragility of biodiversity.

Box 1. The controls over coexistence in systems of two competitors

Coexistence between two species is commonly evaluated with a mutual invisibility criteria, meaning that each species has a positive growth rate when it is at low density and its competitor is at its single species equilibrium (carrying capacity). Such a criteria can only be met when species have greater growth when rare than when common, which requires that individuals are more strongly limiting to individuals of their own species than to individuals of other species[2]. One advantage of this framework is that it can be flexibly applied to systems with stochastic fluctuations in the environment through calculations of the long term average low density growth rate[2].

Chesson[2] has shown how one can decompose species' growth rates when rare into an average fitness difference and stabilizing niche difference between competitors. The average fitness difference describes the degree which one competitor is superior to the other when averaging over the limiting factors in the environment. The precise definition will depend on the model being examined, but in general, reflects the combination of species' innate reproductive capacity in the absence of neighbors, and the degree to which species resist the potentially suppressive effect of neighbors (Supplementary Notes). In the absence of processes that give species advantages when rare, the average fitness difference causes positive growth for the fitness superior and negative growth for the inferior. Tradeoffs that make these growth rates more similar to each other are called "equalizing" mechanisms[2]. Nonetheless, such mechanisms can never cause both species to have positive growth when rare, as required for mutual invisibility. This criterion can only be met with stabilizing mechanisms that arise from niche differences between competitors.

581 Stabilizing niche differences include all factors that cause species to limit individuals of their
582 own species more than they limit individuals of other species[2,83]. These factors increase a
583 species' population growth rate when it drops to low relative abundance[2,83]. Coexistence thus
584 depends on the stabilizing niche difference exceeding the effects of the average fitness
585 difference, such that even the species with an average fitness disadvantage can invade the
586 system. Stabilizing niche differences can arise in well mixed systems if, for example, the two
587 species are limited by different resources or by different specialist consumers or pathogens. They
588 can alternatively arise when species specialize on different locations in a spatially heterogeneous
589 environment or different types of climatic conditions in stochastically fluctuating environments[2].
590
591 One challenge when applying the principles of coexistence theory developed from the mutual
592 invasion condition to systems of three or more competitors is that satisfying this condition is no
593 longer sufficient for predicting coexistence. Even if all species can invade, they may be invading
594 systems without the full complement of resident species if some of those residents depend on the
595 "invader" being common for their persistence[3] (as with rock paper scissors competition). By
596 contrast, in a two species competitive system, the resident species always persists when its
597 competitor is suppressed to the invader state. For this reason, the alternative frameworks for
598 understanding coexistence outlined in Box 2 are particularly important for studying mechanisms
599 that emerge with more than two species.
600
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Box 2. Alternative frameworks for evaluating the stability of coexistence in diverse ecological networks

Although ecological stability is a multi-faceted concept, theoretical approaches for evaluating the stability of species coexistence are traditionally based on the local or global stability of a multispecies equilibrium given specific parameter values. An equilibrium is locally stable, for example, if the system returns to it after an *infinitesimally small* perturbation to species densities, and is determined from the eigenvalues of the Jacobian matrix evaluated at the equilibrium point. For models with a linear functional response, the Jacobean is defined as the product of two terms, the first of which is a matrix whose diagonal elements represent the equilibrium abundances of each species and off-diagonal elements are zero. The second term is the interaction matrix, whose *ij*th entry describes the per-capita effect of changes in the abundance of species *j* on the rate of change of abundance of species *i*. May[20], for example, modeled this matrix as a random matrix in his efforts to define the relationship between diversity and stability in ecological communities. This general approach allows one to relate the ecological concept of stability to a well-defined mathematical framework that is widely used elsewhere in the natural sciences. Higher-order interactions (as defined in the text), can affect local stability by altering the value of the elements of the Jacobian. Global stability, in turn, is a more general concept, quantifying the stability of any potential feasible equilibrium solution after a perturbation of *any given magnitude*[84].

Although the concepts of local and global stability have led to important insights into the behavior of model communities, they have a number of limitations. One is that stability conditions are oftentimes derived for equilibrium solutions that are not necessarily feasible, i.e.,

involve populations with negative abundances. As several authors have pointed out, conditions for feasibility may be stronger than those for local stability, and both have to be simultaneously considered when studying species coexistence[85,86,87,88,89,90]. A second limitation of the local stability approach is the assumption that perturbations only affect species densities. In nature, many perturbations will change species' growth rates or interaction coefficients[91].

An alternative approach that is better suited to addressing multispecies coexistence is structural stability[91,92]. Instead of addressing only the stability of the dynamical variables for a given set of parameter values, this approach quantifies the range of parameter values compatible with the stable coexistence of all species, as determined by the existence of a fixed point which is both fully feasible and globally stable[71,88,90]. It therefore simultaneously considers dynamical stability and feasibility, assumes that perturbations may affect demographic parameters, and is not constrained to small perturbations. It is thus better suited for studies of global environmental change, which often involves large and directional changes. Although less influential in ecology than in other fields, structural stability has been advocated by several ecological theoreticians[39,71,88,89,90,93], and has recently been used to quantify the contribution of indirect interaction chains to multispecies coexistence[94] More generally, it is important to consider how conclusions about the dynamical consequences of interaction chains and higher-order interactions depend on the chosen definition of coexistence and stability.

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653
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663 revisions.
664

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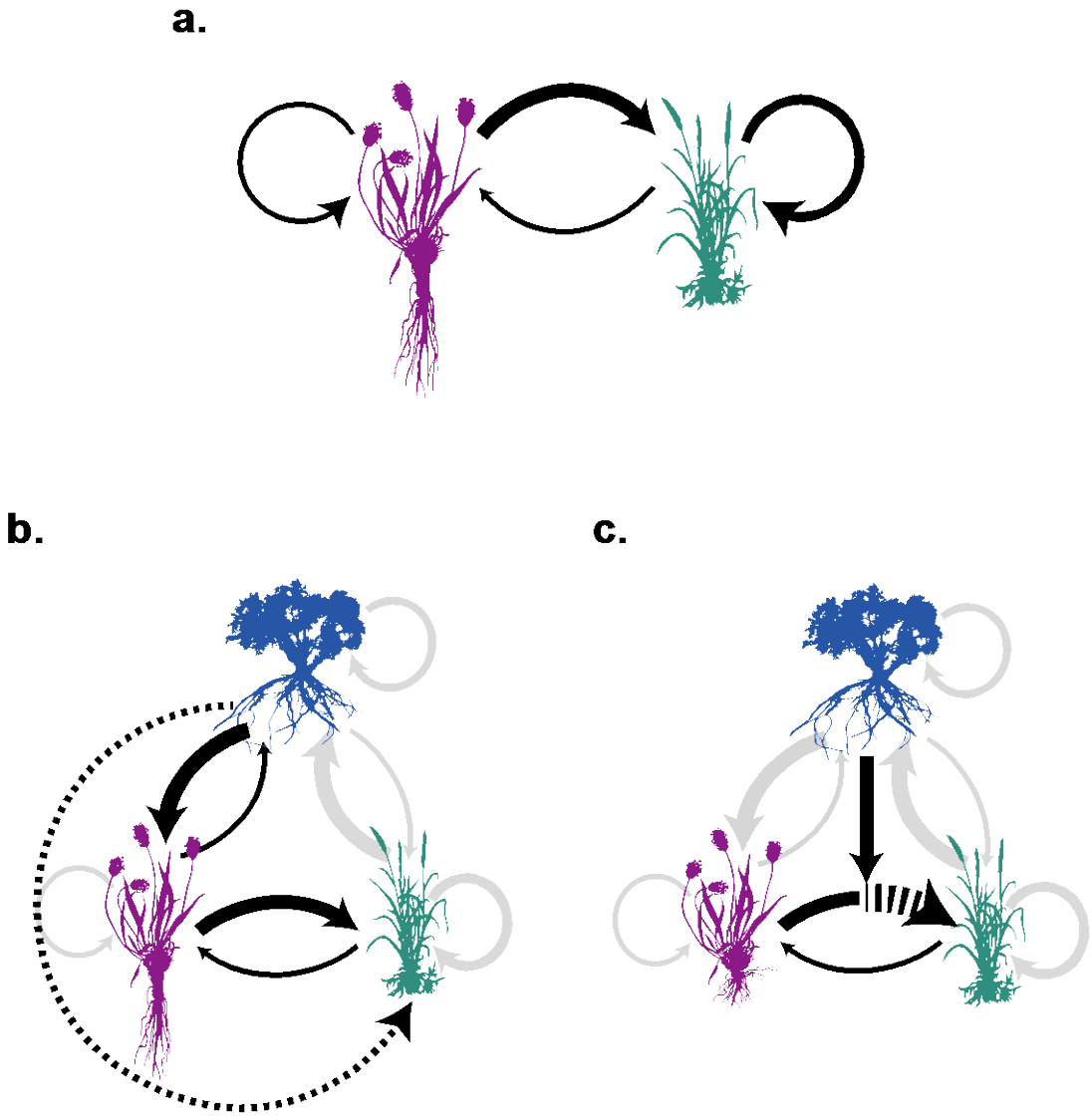

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676 **Figure 1. Coexistence mechanisms that only emerge with more than two competitors.** (a)
677 Strictly pairwise competition between a forb (in magenta) and grass (in green), showing both
678 interspecific and intraspecific interactions. (b) An interaction chain where the shrub (in blue)
679 indirectly benefits the grass via the suppression of the forb (shown by the dashed arrow). (c) A
680 higher-order interaction where the shrub alters the per capita effect of the forb on the grass. In
681 this case, the shrub induces a plastic change in the forb such that it roots at more shallow soil
682 depths, bringing it into greater competitive contact with the grass. Arrow width indicates the
683 strength of the per capita competitive effect.
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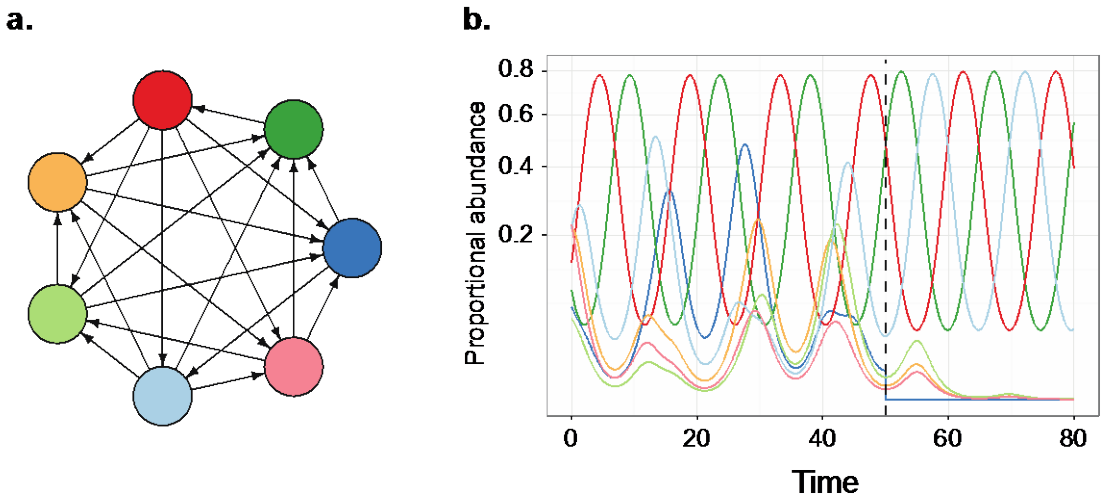

Figure 2. Competitive network and extinction cascade. (a) An intransitive competitive network or "tournament", where arrows point from the winner to the loser in pairwise competition. The system is composed of a number of smaller intransitive loops (e.g. between the light blue, dark blue, and pink species) nested within larger loops that include all seven species (see reference 3 for examples of competitive network structure). (b) Simulation of the dynamics of the system following reference 6. Due to intransitive competitive relationships, the seven species coexist indefinitely, cycling around an equilibrium in which the red and dark green species have density (proportional abundance) 1/3, the light and dark blue species have density 1/9, and the light green, peach, and pink species have density 1/27. At time 50, we send the dark blue species to extinction, and this causes an additional 3 species to go extinct due to the disruption of the intransitivity that stabilized their dynamics. The remaining three species oscillate in a rock-paper-scissors fashion around a density of 1/3. The y-axis is presented on a square root scale to improve the visibility of the low density species.

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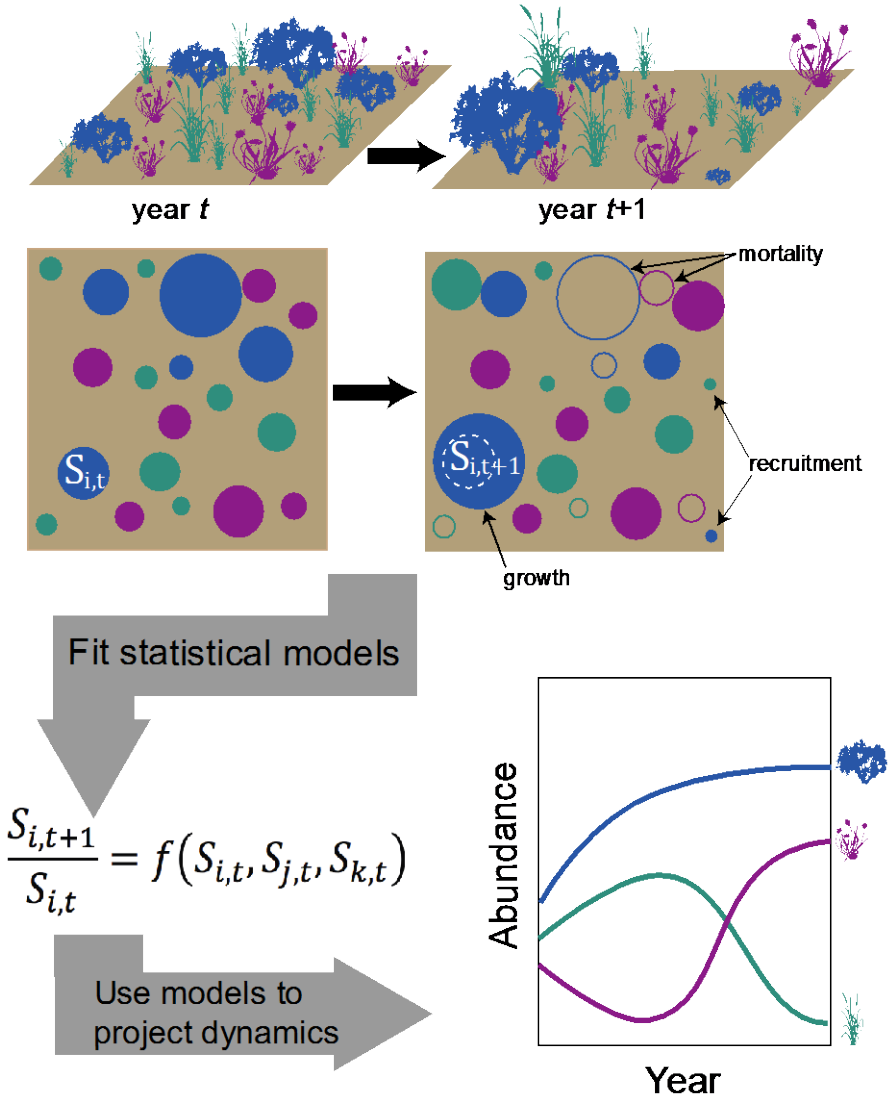

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711 **Figure 3. Data driven modeling approach**. Observational or experimental data can be fit to
712 models, which are then used to analyze the effects of interaction chains or higher-order
713 interactions on dynamics. The first step involves converting between-year patterns of abundance
714 into size or age-based demographic information. For a size-based model, all individuals may be
715 conceived as circles of a given area. The change in size from one year to the next can then be
716 modeled as a function of the abundances or collective size of individuals within a given radius or
717 neighborhood, assuming pairwise or higher-order interactions. Similar models can be built for
718 survival and reproduction. Finally, the fitted functions can be used to inform individual-based or
719 integral projection models of community dynamics. These models and their parameters can be
720 manipulated to add or remove individual coexistence mechanisms, which allows one to evaluate
721 their contribution to diversity maintenance.

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